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Multiple Receivers, Multiple Ornaments, and a Trade-off between Agonistic and Epigamic Signaling in a Widowbird

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ABSTRACT: Sexual displays often involve several different ornamental traits. Yet most indicator models of sexual selection based on a single receiver (usually a choosy female) find that multiple handicap signals should be unstable. Here we study reasons for this contradiction, analyzing signal function, signal content, and trade-offs between signals in the polygynous red-collared widowbird *Euplectes ardens*. Males have both a long, graduated tail and a red carotenoid collar badge. Territory-holding "residents" have slightly shorter tails than the nonbreeding "floaters," but their carotenoid collars are 40% larger, and they have (on the basis of reflectance spectrometry and objective colorimetry) a 23-nm more long-wave ("redder") hue than floaters. This corroborates experimental evidence that the red collar is selected by male contest competition, whereas female choice is based almost exclusively on male tail length. Tail length is negatively correlated with the carotenoid signal, which together with body size and condition explains 55% of the variation in tail length. The trade-off in tail length and carotenoid investment is steeper among residents, suggesting an interaction with costs of territory defense. We propose that the "multiple receiver hypothesis" can explain the coexistence of multiple handicap signals. Furthermore, the trade-off between signal expressions might contribute to the inverse relation between nuptial tail elongation and coloration in the genus *Euplectes* (bishops and widowbirds).

Keywords: sexual selection, status signaling, handicap ornaments, condition dependence, carotenoid coloration, *Euplectes*.

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Many sexual signals are assumed to be quality advertisements with honest-enforcing costs, that is, "handicaps" (Zahavi 1975; Grafen 1990). However, such signals have been difficult to reconcile with "multiple ornaments" (Møller and Pomiankowski 1993) or "multicomponent signals" (Rowe 1999) found in many species. Instead, it has been suggested that multiple ornaments are unlikely to be handicaps. This conclusion is based theoretically on the instability of multiple costly mate choice criteria (Schluter and Price 1993; Iwasa and Pomiankowski 1994; Johnstone 1996) and empirically on the lack of condition-dependent signals expressed in multi- compared to single-ornamented species (Møller and Pomiankowski 1993). These studies have, however, dealt with only a single selection pressure from female mate choice. There are alternative explanations for multiple signals, such as spatially or temporally variable signal selection (see, e.g., Marchetti 1998), and some of these more complex communication scenarios may allow the stable coexistence of handicap signals.

Correlations between signal expression and quality measures, such as condition or health, do not provide unambiguous tests of sexual selection mechanisms (Johnstone 1995). In combination with experimental approaches, however, phenotypic correlations might be informative, if carefully interpreted in the light of life-history perspectives on sexual selection and trade-offs (see, e.g., Höglund and Sheldon 1998; Kokko 2001; Kokko et al. 2002). This also applies to relationships between different signals in the same phenotype. Multiple handicaps are traditionally expected to be positively correlated with each other (e.g., Kodric-Brown and Brown 1984). However, if each handicap signal represents (as theoretically expected) a major investment that is traded off against other life-history investments, it is likely that two such costly investments may create an allocation conflict strong enough to cause a negative phenotypic correlation between the two signals.

Here we explore sexual signal variations and signal

functions in the strikingly multiornamented breeding plumage of male red-collared widowbirds *Euplectes ardens*. In this highly polygynous, sexually and seasonally dimorphic weaverbird, the male nuptial plumage is black with a carotenoid-based (A. Johansson and S. Andersson, unpublished manuscript) red "collar" patch on the chest and a long (ca. 22 cm), graduated tail (Pryke et al. 2001*b*). The red-collared widowbird thus combines two classic avian plumage ornaments with well-documented costs (Balmford et al. 1993; S. Andersson 1994; Hill 1996, 1999; von Schantz et al. 1999; Møller et al. 2000). Previous studies of this species have indicated that these two signals have separate functions: the red carotenoid collar functions as a "status badge" in male contest competition (Pryke et al. 2001*a*, in press), whereas tail length is strongly selected by female mate choice (Pryke et al. 2001*b*; which has also been shown in three other *Euplectes* species; Andersson 1982, 1989, 1992; Pryke and Andersson, in press).

We analyze the variation and fitness consequences of these multiple and presumably costly signals in a wild South African population of red-collared widowbirds. In particular, we compare the morphological and colorimetric variation of territorial "resident" males to a large population of "floaters" (males in nuptial plumage that did not obtain a territory). In addition, we examine the results from a life-history perspective and in relation to current theories for the evolution of multicomponent signals.

Methods

Study Populations and Morphometrics

Male red-collared widowbirds were studied in the Hilton district, KwaZulu-Natal Province, South Africa (29°43′S, 30°17′E), during December 1998 ($n = 41$) and between December 1999 and April 2000 ($n = 116$) and in the Balgowan area (29°35′S, 30°04′E) during April 2000 ($n = 22$). We uniquely color-banded males, excluding red bands to minimize potential effects on color communication (Burley et al. 1982; Metz and Weatherhead 1991). Tarsus length and culmen length were measured to the nearest 0.1 mm, wing length to the nearest 0.5 mm, and body mass to the nearest 0.5 g.

As a measure of overall body size, we used the first principal component (size PC1) derived from and explaining 47% of the variation in tarsus, wing, and culmen length. An index of body condition was computed as the standardized residuals from a linear regression of log (body mass) on 3* log (tarsus length) (S. Andersson 1994), with tarsus length as the preferred measure of skeletal size (Freeman and Jackson 1990). Since the mass/tarsus relationship differed between the three populations (ANCOVA of body mass, tarsus by population interaction; $F = 6.7$, df $= 2, 188$, $P = .002$), we computed a body condition index for each population before pooling, making the measure relative to the population mean rather than the overall mean.

Tail length was measured to the nearest 0.1 mm as the maximum length of the folded tail. Fluctuating asymmetry (FA) of the longest pair of rectrices was calculated as the absolute left-right difference divided by their average length (Palmer and Strobeck 1986; Møller and Höglund 1991). Birds with broken, missing, or growing feathers were excluded from the FA analyses. Collar area was estimated as the product of the maximum width and the average of three height measures (left, central, and right; to the nearest 0.1 mm). Collar asymmetry was computed as above for the left and right side height measures. In the Hilton 99/00 population, where 57 males were captured more than once and remeasured, repeatabilities (Lessells and Boag 1987) were significant for all measurements ($F = 6.2$–21.6, $r = 0.81$–0.96, $P < .001$).

Reflectance Spectrometry and Colorimetrics

The proximate basis of the red color signal is a mixture of three carotenoid pigments in the feathers (lutein, zeaxanthin, and canthaxanthin; A. Johansson and S. Andersson, unpublished manuscript). Spectral reflectance (at ± 2 nm resolution) of the red collar was measured with a PS1000 spectrometer (Ocean Optics, Dunedin, Fla.), a HL2000 halogen light source, a WS-2 white reference, a fiber-optic reflectance probe (Avantes, Eerbek, Netherlands), and C-spec software (Ancal, Las Vegas, Nev.). The probe was fitted with a matte black tube that shielded out external light and standardized the measuring distance. The probe was held (not pressed) against the plumage, scanning specular reflectance from a 4-mm-wide circle. Five consecutive scans (removing the probe between each) preceded by a reference scan for each individual were taken from the center of the collar patch.

Objective indices of the three main dimensions of color signals (spectral intensity, location, and purity; Hailman 1977) were computed from the five scans and averaged for each individual. Spectral intensity (brightness) was estimated by $R_{350–700}$, the sum of reflectance from 350 to 700 nm. Spectral location (hue, here referred to as "redness") was estimated as ($\lambda[R50]$), the wavelength at which reflectance is halfway between its minimum (R_{min}) and its maximum (R_{max}). Spectral purity (chroma) has a more complex dependence on several aspects of reflectance shape, such as slope height and steepness. Like Pryke et al. (2001*a*), we used individual ($\lambda[R50]$) as the segment divider and computed chroma (C_{R50}) as $(R_{350–\lambda(R50)} - R_{\lambda(R50)–700})/R_{350–700}$. However, a simpler and not segment-based measure of chroma $[(R_{max} - R_{min})/(R_{avg})]$ gave qualitatively identical

results. Further details on the methods used to measure and analyze reflectance are described in Pryke et al. (2001*b*).

Statistical Methods

For relationships involving the strongly skewed fluctuating asymmetry measures, Spearman rank correlations were used. In all other cases, parametric tests were used since variables were approximately normal and residual variances uniform (and not extrabinomially distributed in the case of logistic regressions). In multiple regressions, multicollinearity was not strong enough to affect the analyses (Mitchell-Olds and Shaw 1987), as judged by the ratios of eigenvalues from the covariance matrix of the standardized independent variables (Fry 1993). Two-tailed significance tests were used throughout.

Results

Signal Expression in Residents and Floaters

As an indication of which signal traits are involved in (i.e., selected by) male-male contest competition over territories, we compared the morphology and colorimetrics of floaters and residents (table 1). Tail length, the main mate choice cue (Pryke et al. 2001*b*), was almost significantly ($P = .065$) shorter in residents and thus seems unimportant as an agonistic signal. In contrast, the expression of the carotenoid signal was in several respects stronger in residents (table 1); it was 40% larger, tended to be more symmetric, and was significantly "redder," primarily through a 23-nm more long-wave hue ($\lambda[R50]$; fig. 1). Objective chroma and brightness, both of which were related to hue ($r = 0.40$ and -0.59, respectively, $n = 71$, $P < .001$) also differed, but less dramatically. Residents were also larger (tarsus length and size PC1) and heavier, both absolutely (body mass) and relatively (i.e., condition; see "Methods"). Several of the traits above were significantly intercorrelated. Collar area was positively correlated with redness ($r = 0.75$, $n = 68$, $P < .001$), body mass ($r = 0.29$, $n = 118$, $P = .001$), and body size PC1 ($r = 0.19$, $n = 118$, $P = .03$) but negatively related to tail length ($r = -0.42$, $n = 114$, $P < .001$) and collar asymmetry ($r = -0.36$, $n = 118$, $P < .001$; see "Signal Trade-Offs" below). To identify independent effects of the variables on male contest competition, we used logistic regressions with male status (floater or resident) as the response variable. The best model accounted for 81% of the binomial variance and included a dominant effect of collar area, a significant but weak effect of body size, and a barely significant ($P = .037$) effect of body condition (table 2). As in standardized selection analysis (Lande and Arnold 1983), variables were standardized to 0 mean and unit variance, meaning that coefficients denote effects of 1 SD of each independent variable on the odds of territory ownership. Thus, changing collar area by 1 SD increases the probability that a male is a resident 120-fold. In comparison, changing body size by 1 SD increases that probability ninefold; changing body condition, only 2.7-fold. Replacing collar area with redness produced a similar but slightly weaker model ($R^2 = 72\%$). We can thus conclude

Table 1: Variation in signal traits, morphology, and body condition between floater and resident red-collared widowbird males

		Floaters			Residents				
Trait	Measure or unit	Mean	SD	*n*	Mean	SD	*n*	*F*	*P*
Red collar:									
Area	Width × height	195.1	±34.81	78	274.2	±25.12	40	163.3	<.001
Asymmetry	$\lvert(L-R)\rvert$/mean height	.014	±.02	78	.009	±.01	40	3.9	.051
Hue ("redness")	$\lambda(R50)$	557.2	±14.73	38	580.3	±2.72	33	50.1	<.001
Chroma	C_{R50}	.54	±.10	38	.59	±.09	33	5.3	.025
Brightness	$R_{350-700}$	94.6	±18.03	38	82.1	±25.64	33	5.8	.019
Tail:									
Tail length	mm	225.5	±24.6	76	215.6	±31.92	40	3.5	.065
Tail asymmetry	$\lvert(L-R)\rvert$/mean length	.100	±.22	69	.068	±.17	37	.6	NS
Morphology:									
Tarsus length	mm	23.7	±.42	81	24.5	±.29	41	110.4	<.001
Wing length	mm	76.6	±1.83	81	77.3	±1.33	41	5.9	.016
Culmen length	mm	14.1	±.37	81	14.2	±.38	41	.7	NS
Body size	PC1	−.2	±.83	81	.7	±.86	41	33.8	<.001
Body mass	g	20.2	±1.11	81	21.6	±1.01	41	42.9	<.001
Body condition	Residual mass index	−.009	±.05	81	.017	±.05	41	6.6	.012

Note: *F* values and significance levels are derived from one-way ANOVAs.

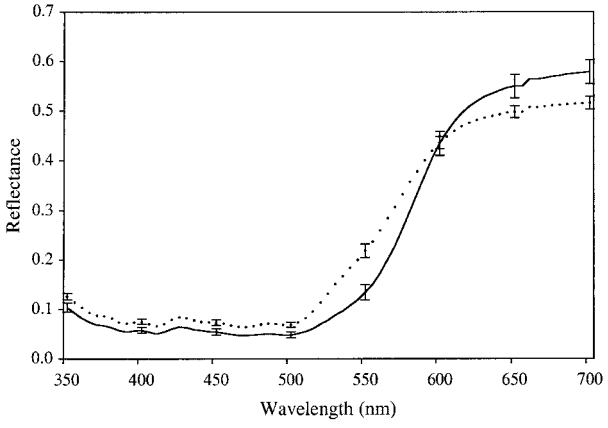

Figure 1: Average spectral reflectances (with standard error bars) of the red carotenoid plumage (collar) in male red-collared widowbirds identified as either floaters ($n = 38$; *dashed line*) or residents ($n = 33$; *solid line*).

that male agonistic competition exerts a strong selection pressure on the red collar signal.

Signal Trade-Offs

Costly acquisition and modification of carotenoids, as well as physiological allocation conflicts (e.g., Olson and Owens 1998), should lead to a trade-off between the size and redness of the color signal. In other words, a given amount of pigment may be used for a small, intensely colored patch or for a large patch with more diluted coloration. This presumed trade-off does not appear as a negative phenotypic correlation in the red-collared widowbirds. Instead, collar area was positively correlated with redness ($r = 0.75$, $n = 90$, $P < .001$) and chroma ($r = 0.33$, $n = 90$, $P = .001$), as would be expected if total investment (i.e., carotenoids) varies substantially among individuals (van Noordwijk and de Jong 1986). In contrast, there was a phenotypic trade-off (negative correlation) between tail length and both collar area ($r = -0.40$, $n = 135$, $P < .001$) and redness ($r = -0.31$, $n = 119$, $P < .001$) in both study populations. Using multiple regressions of tail length against all other traits (listed in table 1), we investigated which of the two correlated aspects of the carotenoid display (area and redness) had the strongest effect. Both forward and backward stepwise procedures (F to enter $= 4$, F to remove $= 3.9$) resulted in the same three independent variables entering the model ($F = 55.3$, df $= 1, 133$, $P < .001$, $R^2 = 55.1\%$): wing length (standardized $b = 0.57$, $t = 9.5$, $P < .001$), collar area ($b = -0.37$, $t = 6.4$, $P < .001$), and body condition ($b = 0.19$, $t = 9.5$, $P = .002$). Thus the trade-off between tail length and carotenoid display remained when correlated traits were controlled for. Furthermore, the model was similar when collar redness was used instead of collar area ($F = 33.0$, df $= 3, 87$, $P < .001$, $R^2 = 52.5\%$), further indicating that the two different measures are positively covarying aspects of the carotenoid display.

To investigate whether male status had a confounding effect, we tested the trade-off in an ANCOVA with tail length as the dependent variable, collar area as the covariate, and territory ownership status as the cofactor. In this model, the overall effects of collar area and male status were significant and, most interestingly, so was the interaction term (ANCOVA; collar area: $F = 36.8$, df $= 1, 110$, $P < .001$; territory ownership: $F = 9.2$, df $= 1, 110$, $P = .003$; collar by territory interaction: $F = 6.8$, df $= 1, 110$, $P = .010$). Although the test of slope homogeneity might be dubious because of the bimodal distribution of the covariate, it seems that residents have a steeper signal trade-off than floaters. This was also indicated by separate standardized linear regressions (residents: standardized $b = -0.59$, $t = -4.4$, $P < .001$; floaters: standardized $b = -0.43$, $t = -4.0$, $P < .001$; fig. 2). That the relationship was significant in each group also indicates that the trade-off was not just an effect of floaters and residents adopting discrete strategies (i.e., small-collared, long-tailed floaters and large-collared, short-tailed residents) but rather a continuous trade-off that seems stronger among the residents (see "Discussion").

Condition Dependence and Signal Content

To test whether aspects of multiple signaling predicted male body condition (see "Methods"), we used multiple stepwise regression with condition as the dependent variable and signal traits (table 1) as the independents. Only tail length entered the model as a significant positive predictor of condition ($b_{\text{TAIL}} = 0.28$, $F = 14.3$, df $= 1, 174$, $P < .001$,

Table 2: Traits affecting male status as floater or resident

Trait (standardized)	Exp[coeff]	χ^2
Collar area	120.4	87.9***
Body size PC1	9.1	17.1***
Body condition	2.7	4.3*

Note: Results obtained by logistic regression of male status on three standardized (0 mean and unit variance) traits. Exp[coeff] values can be interpreted as the increased probability of territory ownership associated with a trait change of 1 SD (full model: $R^2 = 81\%$, $n = 118$).

* $P = .037$.

*** $P < .001$.

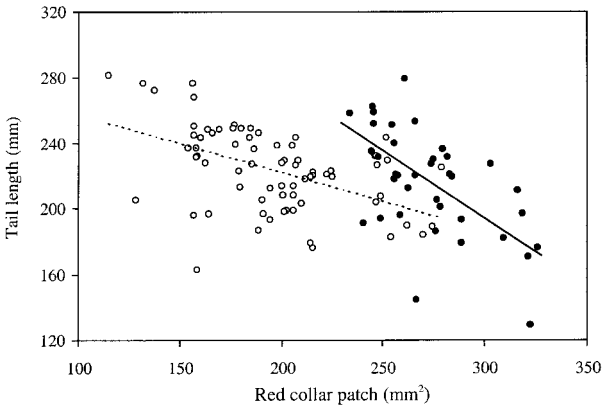

Figure 2: Signal trade-off (negative phenotypic correlation) between tail length and collar area in red-collared widowbirds. The negative relationship is present both in the floaters (*open circles*) and in residents (*filled circles*). Linear regression lines: floaters, tail length = 283.8 − 0.30 × collar area, $F = 16.2$, df = 1, 74, $P < .001$, $R^2 = 17.1\%$; residents, tail length = 421.1 − 0.75 × collar area, $F = 19.3$, df = 1, 38, $P < .001$, $R^2 = 32.5\%$. For ANCOVA demonstrating significantly different slopes in the two groups, see text.

$R^2 = 7.1\%$). However, collar redness was included as a nearly significant and positive partial predictor of body condition ($b_{TAIL} = 0.32$, $t = 3.4$, $P < .001$; $b_{1(R50)} = 0.16$, $t = 1.8$, $P = .08$; $F = 6.0$, df = 2, 117, $P = .003$, $R^2 = 7.8\%$). This suggests that long tails and, to some extent, redder collars directly indicate current body condition. However, while true for floaters ($b_{TAIL} = 0.58$, $t = 3.6$, $P =< .001$; $b_{1(R50)} = 0.28$, $t = 1.8$, $P = .09$; $F = 6.8$, df = 2, 34, $P = .004$, $R^2 = 25.4\%$), this signal content was absent in the resident males ($b_{TAIL} = 0.19$, $t = 1.0$, $P = .33$; $b_{1(R50)} = -0.17$, $t = -0.89$, $P = .38$; $F = 1.5$, df = 2, 31, NS, $R^2 = 3.3\%$). In other words, except for their on average better condition than floaters (table 1), the variation in tail length among residents did not seem to advertise their current body condition.

Fluctuating asymmetry might also indicate signal content (e.g., stress or "developmental stability"; Parsons 1990). However, tail asymmetry showed no relationship with tail length ($r_s = -0.06$, $n = 157$, NS) or any other morphological trait ($r_s = -0.13$–0.09, $n = 129$–157, $P = .17$–$.82$; see also Goddard and Lawes 2000; Pryke et al. 2001*b*). A weak negative correlation with condition ($r_s = -0.15$, $n = 157$, $P = .054$) could imply that tail asymmetry itself is a sexually selected quality signal, but this is refuted as regards both female choice (Pryke et al. 2001*b*) and male-male competition (this study). Collar asymmetry was, however, negatively correlated with both collar area (see above) and redness ($r_s = -0.26$, $n = 68$, $P = .031$), which might be taken as support for a quality message of the carotenoid display (Hill 1998).

Discussion

Agonistic Sexual Selection of Carotenoid Coloration

Although recent studies of carotenoid signals have emphasized their role in female mate choice (see, e.g., Hill 1999), there are many cases in fishes and birds in which red carotenoid displays function in agonistic signaling among males. Examples include skin color in sticklebacks (e.g., Bakker and Sevenster 1983) and cichlids (Evans and Norris 1996), plumage patches in red-winged blackbirds and malachite sunbirds (e.g., Hansen and Rohwer 1986; Evans and Hatchwell 1992*a*), combs and wattles in galliform birds (e.g., Mateos and Carranza 1997), and, in more recent work on birds, red plumage in northern cardinals *Cardinalis cardinalis* (Wolfenbarger 1999) and beak color in red-billed queleas *Quelea quelea* (Shawcross and Slater 1983; Dale 2000). In red-collared widowbirds, floaters and residents differ markedly in both the area and redness of their carotenoid badge, revealing an effect of carotenoid signal variation in male contest competition. Together with both field and captive experiments (Pryke et al. 2001*a*, in press), this represents a strong case for "carotenoid status signaling" in a bird species.

The Multiple Receiver Hypothesis

Predictions that multiple handicap signals should converge on the single most efficient signal (Schluter and Price 1993; Iwasa and Pomiankowski 1994; Johnstone 1996) typically involve integrated signals that are simultaneously perceived by a single receiver (the choosy female). However, different kinds of receivers (or otherwise spatially or temporally variable signal selection; Marchetti 1998) may exist. We suggest that such situations be collectively referred to as the "multiple receiver hypothesis." In sexual selection, mates and rivals may assess different signals, which thereby do not compete for the same receiver's attention. Consequently, both ornaments might be stable condition-dependent signals, reflecting similar or different qualities and associated costs. These two kinds of signals may therefore be maintained because they are directed at different receivers, hence affecting different components of fitness (e.g., resources and mates, respectively). The distinction between sexual contest competition and mate choice is well established in sexual selection theory (see, e.g., M. Andersson 1994), but it deserves additional attention as a potential multiple receiver explanation for several costly ornaments in the same phenotype. Furthermore, if different receivers are receptive to different aspects or dimensions of the same signal (such as repertoire size and length of song, or pattern and color of visual displays), display complexity might increase as a consequence of such

dual "armament-ornament" functions of exaggerated displays (Berglund et al. 1996).

Coexistence of distinctly different signals used in mate choice and male aggressive competition have been demonstrated or strongly indicated in a number of insects, frogs, and birds (M. Andersson 1994). Our results are similar to those found in the scarlet-tufted malachite sunbirds *Nectarinia johnstoni*, in which elongated tail streamers are favored by female choice and red pectoral tufts by male aggressive competition over territory size (Evans and Hatchwell 1992*a*, 1992*b*). In spite of this and several other examples of separate inter- and intrasexual signals, multiple receivers (e.g., mates, rivals, predators) have rarely been explicitly discussed in the context of multiple ornaments (but see, e.g., Marchetti 1998). The present results provide evidence for a multiple-receiver function of the carotenoid and tail signals in red-collared widowbirds, the different receivers being male rivals and female mates, respectively.

A Trade-off between Handicap Signals

For any reproductive investment, a trade-off with other life-history parameters is expected (e.g., Williams 1966; Stearns 1992). Such trade-offs for costly sexual ornamentation and behaviors will create variation in the optimal signal expression, that is, the essence of honest signaling. Trade-offs between sexual signals and other life-history traits have been revealed in many organisms (e.g., Møller 1989; Gustafsson et al. 1995; Mappes et al. 1996; Zuk et al. 1998; Brooks 2000; Galen 2000; Griffith 2000). Depending on how closely a phenotypic "quality" measure (e.g., condition, survival) is related to this life-history parameter, the correlation with the signal can either be positive, zero (cancelled out), or negative (Johnstone 1995). Although positive relationships between signal traits and condition suggests quality advertising, a lack of or negative correlations are not necessarily evidence against it (Kokko 2001). A negative correlation may simply indicate that the mating benefits are so large that the optimal advertisement levels of high-quality males reduce their survival compared to low-quality males (Kokko 2001).

Of particular interest is what happens when a second condition-dependent signal is added. The earlier studies of multiple quality advertisements have considered signals that were assumed to be positively correlated with quality and, therefore, also with each other (e.g., Kodric-Brown and Brown 1984; Evans and Hatchwell 1992*b*). From a life-history perspective, however, multiple handicap traits (for a given condition) should trade off against each other and might also influence the trade-off between total signaling investment and survival. Therefore, multiple handicap signals, if they are truly separate and vary relative to each other and if individuals do not vary much in quality or condition, are likely to show a negative phenotypic correlation. Conversely, when two signals are positively correlated (such as collar area and redness), they may have become developmentally integrated to the extent that they can only vary little relative to each other compared to the larger variation in quality among individuals (see, e.g., van Noordwijk and de Jong 1986; Stearns 1992).

Mechanisms behind the Signal Trade-Off

The negative correlation between the signals suggests that the allocation between the traits varies more than the total investment (see, e.g., fig. 4.8 in Stearns 1992). But what mechanism is responsible for this variable allocation? One possibility is that there are two (or more) male tactics with different emphasis of agonistic or epigamic signaling, respectively. As far as we currently understand this system, however, there seems to be little scope for distinct alternative signaling tactics. This is because both a territory and a long tail seem crucial for mating success. In other words, a male without a territory is likely to have no mating success no matter how long his tail, and a short-tailed territorial male has low mating success regardless of his territory size or quality (Pryke et al 2001*b*). This suggests that an optimal strategy should be to invest enough in agonistic signaling (collar patch) to obtain a territory and then invest the rest in epigamic signaling (tail length) to attract females. Factors that could create alternative strategies, such as extra-pair fertilizations obtained by long-tailed floaters or large-collared neighbors, or different trade-offs with survival or future reproduction, remain to be investigated.

There are two main proximate mechanisms by which the negative phenotypic correlation between carotenoid coloration and tail length may have arisen. First, individual variation in relative allocation between the two signals may exceed the individual variation in condition and total optimal investment mentioned above, resulting in a negative correlation. Such large variations in signal allocation might be maintained by frequency-dependent or fluctuating selection pressures. Further studies are needed to show whether such strategic variation in signal allocation exists in red-collared widowbirds.

Regardless of whether different signaling strategies could cause a polymorphism in signal allocation, the allocation conflict itself might be strong enough to create a negative phenotypic correlation between the signals. In other words, the variation in allocation for a given male condition or quality (e.g., health or acquired resources) is large compared to the variation in quality along a given allocation trajectory. This might be the case in red-collared widowbirds, owing to a strong allocation conflict between

the two signals. The molt to long tails, temporally overlapping with intense territorial competition, is fast and stressful as judged by frequent fault bars and rapid growth in this species (S. Andersson and S. Pryke, personal observations) and in Jackson's widowbird (S. Andersson 1994). There are several potential conflicts between the physiological cost of molt (e.g., Lindstrom et al. 1993; Schieltz and Murphy 1997; Svensson and Nilsson 1997) and carotenoid pigmentation (e.g., Olson and Owens 1998; Hill 1999; Møller et al. 2000). For example, vitamin A and other retinoids are important growth factors (Goodwin 1986), irreversibly metabolized from ingested carotenoids that are also required for the plumage pigmentation. Furthermore, parasites and other immune challenges may affect rapid tail growth as well as carotenoid uptake and usage (Møller et al. 2000). Such factors might further escalate the conflict between the two signal investments.

The apparently steeper trade-off among residents suggests that the costs of territory acquisition, defense, and display interact with the production of costly plumage signals, in particular, tail growth. While the red collar is part of the body molt just before territorial competition begins (which makes sense, since the red collar is essential for male contest competition), the long tail continues to grow for several weeks after territories are established (S. Andersson and S. Pryke, personal observations; S. Andersson 1994). Territorial defense and display are likely to be costly, which may explain the reduced tail growth in residents compared to floaters. Jackson's widowbird provides a striking parallel; court holders on leks showed a steeper and continuous decline in condition during tail growth, whereas floater condition decreased less steeply and also seemed to recover after tail completion (S. Andersson 1994).

In conclusion, an interesting scenario emerges in which successful males must first develop a carotenoid signal large and red enough to obtain a territory. Thereafter, most of the remaining investment can be allocated to tail growth, since females seem to have an open-ended preference for this trait (see also Pryke and Andersson, in press). However, caution needs to be invoked as the data presented is correlative and experiments are required to substantiate these results. Further work is also needed to show how this allocation problem is solved and whether red-collared widowbird males vary in signal allocation strategy.

Comparing the *Euplectes* species, we find an inverse relationship between tail length and carotenoid coloration—a striking feature of their interspecific variation in nuptial plumage. The widowbirds have elongated tails but little or no carotenoid pigmentation, and the bishops have short tails but extensive yellow or red plumage (Craig 1980; Andersson and Andersson 1994). A direct energetic trade-off between the two signals may therefore have been an important constraint in the diversification of their nuptial plumages. Furthermore, if the signal functions are the same in most *Euplectes* species, it is possible that the plumage diversity can be explained in part by differences in the balance between agonistic and epigamic selection pressures. For example, the small and densely packed reedbed territories of the bishops (see, e.g., Craig 1980) may lead to strong contest competition, explaining their conspicuous carotenoid color displays. The larger and more dispersed territories of widowbirds may involve a stronger emphasis on sexual selection through female choice of long tails.

Conclusion

The multiple receiver hypothesis, in which different signals are selected by separate receivers, may explain the coexistence of costly ornaments. In male red-collared widowbirds, the long tail is favored by female mate choice, and the red carotenoid collar (size and redness) is used in territorial competition. This is evident from the larger and redder collars of territory-holding males (this article) and from previous experiments (Pryke et al. 2001*a*, in press). The signals are strongly negatively correlated with each other, especially among territory-holding males. This pattern may arise from a direct physiological allocation conflict between the traits, a conflict that appears strongest among territorial males for whom costly territory defense and sexual displays may constrain tail growth. Contrary to traditional views, we suggest that such a signal trade-off does not contradict handicap signaling but is, rather, expected if both signals are costly quality advertisements, that is, multiple handicap signals.

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